The Ternifolia Group of *Macadamia* Species[1]

W. B. Storey[2]

The genus *Macadamia* (family Proteaceae), as presently understood, comprises ten species of tropical and subtropical evergreen trees (Storey, 1959). One species, *M. hildebrandii* Steenis, is native to Celebes. Three species, *M. rousselii* (Veill.) Sleumer, *M. veillardii* (Brongn. and Gris.) Sleumer, and *M. francii* (Guill.) Sleumer, are native to New Caledonia. The remaining six species, *M. whelani* (F. M. Bail.) F. M. Bail., *M. ternifolia* F. Muell., *M. integrifolia* Maiden and Betche, *M. tetraphylla* L.A.S. Johnson, *M. prealta* (F. Muell.) F. M. Bail., and *M. heyana* (F. M. Bail.) Sleumer, are native to eastern Australia. *M. ternifolia* is the type species upon which von Mueller (1858: 72) established the genus in 1858.

The species of *Macadamia* fall naturally into four distinct intrageneric groups. Group 1: The three extra-tropical Australian species, *M. ternifolia, M. integrifolia,* and *M. tetraphylla.* Group 2: The two extra-tropical Australian species, *M. prealta* and *M. heyana.* These species were considered by early botanists to belong to the allied genus *Helicia.* Group 3: The two tropical species of northeastern Queensland and Celebes, *M. whelani* and *M. hildebrandii,* respectively. Group 4: The three tropical New Caledonian species, *M. rousselii, M. vieillardii,* and *M. francii.* Until they were transferred to *Macadamia* by Sleumer (1955:4–5) in 1955, these species had been placed in the genus *Roupala.*

Regardless of how the members of the three latter groups have been placed generically, there seems to have been no question about their identities as clear-cut, easily recognized species. The identities and typifications of the three species comprising Group 1, however, seem to have become confused almost immediately after von Mueller established the genus *Macadamia,* with the collection of additional material by various botanists, all of which ended up in herbariums as *M. ternifolia.* The first break in this confusion came with the realization by Johnson (1954:15–18) that the species which, as *M. ternifolia,* as early as 1870 (Anonymous, 1870:1811) had been brought into cultivation in Australia for its edible nuts, was not von Mueller's *M. ternifolia* at all but, instead, was a species which had never been properly described botanically. Consequently, Johnson described it as a new species, *M. tetraphylla.*

The second break came in 1956 when Smith (1956:39–40) recognized that the species which Maiden and Betche (1897:624) described as a new species, *M. integrifolia,* but which later they revised (Maiden and Betche, 1899:150) to *M. ternifolia* var. *integrifolia,* was indeed a valid species in its own right. At the same time, Smith clearly typified *M. ternifolia.* In so doing he pointed out that the species described as *M. minor* and *M. lowii* by F. M. Bailey (1910:11; 1911:127) are only variant forms of *M. ternifolia,* and that the names, therefore, must lapse into synonymy.

In view of the confusion which existed in the past, and which continues to some extent today, especially in horticultural literature, I shall summarize and compare here the salient features of the three species in question, with the hope that this will clarify the delineations which separate the taxons of this so-called *ternifolia* group.

TYPIFICATION

The principal taxonomic characters of the three species under discussion are listed in Table 1. Additional notes are given below.

M. ternifolia

VERNACULAR NAMES: Gympie nut; Maroochy nut; small-fruited Queensland nut.

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[2] Department of Horticultural Science.

INDIGENOUS RANGE: Tropical rainforests of Australia on the eastern slope of the Great Dividing Range, extending from the Pine River northwest of Brisbane in the Moreton Bay District of Queensland northward to Kin Kin in the Gympie District, a distance of about 130 miles; latitudinal range, about 27°30′–26° S. I saw trees in their native habitat in the Blackall Range near Maleny and in the vicinity of the near-coastal village of Eumundi.

Trees of this species are small in comparison with the other two, seldom attaining heights and spreads exceeding 15 ft. They have a tendency to develop multiple trunks. As noted by Smith (1956:39) "the species is quite distinctive in the field with its smaller leaves, which are reddish on the young shoots, more slender and dark branchlets, pinkish flowers and smaller fruits." The flowers are borne in short subterminal axillary racemes on mature terminal

TABLE 1
PRINCIPAL TAXONOMIC CHARACTERS OF *M. ternifolia*, *M. integrifolia*, and *M. tetraphylla*

CHARACTER	*M. ternifolia*	*M. integrifolia*	*M. tetraphylla*
Phyllotaxy	basically, 3 leaves in a nodal whorl; young seedlings may have only 2; occasional branches have 3 or 5	basically, 3 leaves in a nodal whorl; young seedlings usually have only 2; occasional branches have 4	basically, 4 leaves in a nodal whorl; young seedlings usually have only 2; occasional branches have 3 or 5
Leaf attachment	petiolate	petiolate	sessile or scarcely subsessile
Adult leaf shape	lanceolate	oblanceolate to obovate	oblanceolate
Adult leaf margin	scarcely serrate, with 8–10 teeth on side	generally entire; sometimes with 1–12 teeth on a side	numerous serrations, ranging from 15–40 on a side; occasional leaves have fewer than 15
Color of new growth	pink to red	pale green; occasional individuals with bronze tinging	pink to red; occasional individuals yellowish-green, due to lack of anthocyanin
Flower color	pink	white	pink; white or cream colored in individuals lacking anthocyanin
Racemes	2–5 inches long, with 50–100 flowers	4–12 inches long, with 100–300 flowers	6–18 inches long, with 100–300 flowers
Pericarp	grayish-green in appearance due to dense white pubescence; dehisces fully on tree before fruit drops	bright clear green, due to nearly glabrous condition; often fails to dehisce when fruit is still on tree	grayish-green in appearance, due to fairly dense white pubescence; dehisces fully on tree before fruit drops
Seed size	transverse diameter ⅜–¼ inch	transverse diameter ½–1¼ inches	transverse diameter ½–1½ inches
Seed shape	commonly fusiform to nearly spherical	commonly spherical	commonly fusiform, some nearly spherical
Seed surface	smooth to scarcely pebbled	generally smooth; rarely with slight pebbling	generally pebbled; infrequently smooth or nearly so
Kernel	bitter; unpalatable	sweet; highly palatable	sweet; highly palatable

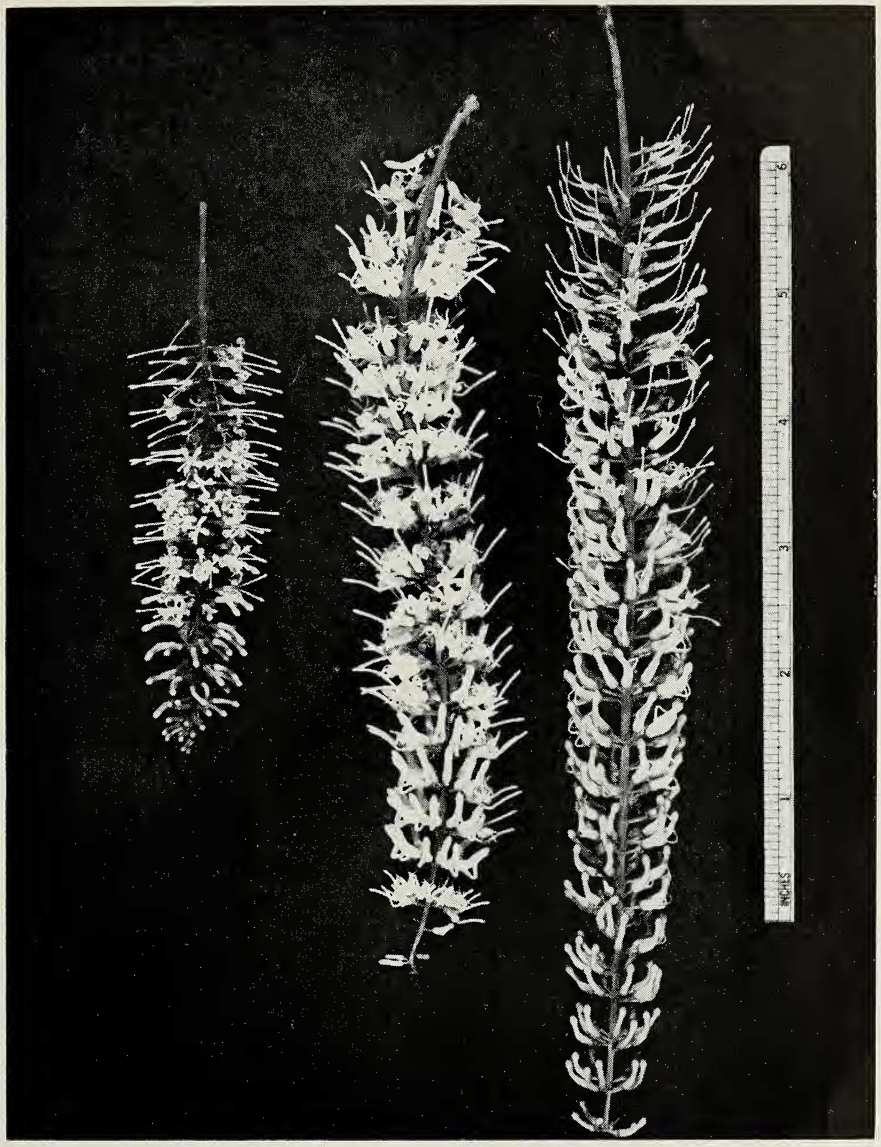

FIG. 1. Racemes of *Macadamia* species. *Left, M. ternifolia; center, M. integrifolia; right, M. tetraphylla.*

branchlets. The racemes rarely exceed 5 inches in length, with an upper limit of about 100 flowers (Fig. 1). The follicular fruits mature and drop in April in Australia, in November in California. The species is not ordinarily cultivated because the nuts are so bitter that they are unpalatable. They are small in comparison with those of the other species (Fig. 2). The leaves are small, rarely exceeding 6 inches in length and 1 inch in width. The transition which occurs in leaf form from seedlings of newly initiated branch shoots to the adult, fruiting branch is shown in Figure 3*A*. The leaves occur in nodal whorls of three to five, but young seedlings may have them initially only in opposite pairs.

Much of the misidentification and confusion among the species resulted from the mixing of transitional forms in the herbarium. A more detailed discussion of leaf forms and variations in nodal numbers has been published elsewhere (Storey, 1963).

It seems unlikely that this species occurred anywhere outside of Australia until the writer introduced it into California in 1960. Pope (1929:3) thought that certain trees on the island of Hawaii belonged to this species, and, because of the bitterness of their nuts, urged their destruction to prevent them from hybridizing with the other two species. I was closely associated with Pope at the time, and was familiar with the trees in question. Having seen both *M. ternifolia* and *M. integrifolia* in their native habitats and under cultivation, I am reasonably certain that the trees in question were not the first species but were a form of the latter in which some bitterness had developed. Bitterness is known to occur in some seedling lines of the species.

M. integrifolia.

VERNACULAR NAMES: Macadamia nut; smooth-shell macadamia nut; Queensland nut; Australian nut; bush nut; nut oak; Bauple nut (sometimes spelled as pronounced, Bopple, or corrupted to Popple).

INDIGENOUS RANGE: Coastal and tropical rainforests on the eastern slopes of the Great Dividing Range in Queensland, extending northward from the Numinbah Valley, which lies immediately to the north of the McPherson Range of mountains that forms the boundary between Queensland and New South Wales, to the lower Mary River near Maryborough, a distance of about 275 miles; latitudinal range, about 28°–25° S.

The trees of this species are large and spreading, some attaining heights of 60 ft or more and spreads of 50 ft. The branchlets are lighter colored than those of *M. ternifolia.* New flushes of growth generally lack any reddish or pinkish coloration. Juvenile leaves are long, linear-lanceolate, the adult leaves usually becoming entire or nearly so (Fig. 3*B*). Adult leaves measure 4–12

FIG. 2. Seeds of *Macadamia* species. *Top, M. ternifolia; left, M. integrifolia; right, M. tetraphylla.*

inches in length and 1–3 inches in width. They occur in whorls of three or four, with three by far the most common. Young seedlings and new shoots may have them in opposite pairs. The inflorescences are borne on mature branchlets, usually on the growth increments produced in the top two or three, or more, seasons preceding the most recently matured ones. The flowers are white. The racemes upon which they are borne vary among individuals, from as short as 4 inches to as long as 12 inches or more. The number of flowers on the racemes ranges from 100 to 300 (Fig. 1). The bulk of the crop matures from March to June in Australia, July to November in Hawaii, and November to March in California. However, some fruit is produced almost every month in the year, consequently the species is sometimes called "everbearing."

Although this species was not recognized as new and given a specific epithet until 1897 (Maiden and Betche, 1897:624), it was introduced into California as a potential economic plant, under the invalid name *M. ternata,* in 1879 by the University of California College of Agriculture (1881:66) and planted on the campus at Berkeley in 1882 (Butterfield 1963: 48). Two trees of this introduction continue to grow on the Berkeley campus. Almost simultaneously, at a time reported to be between 1881 and 1885 (Pope 1929:2; Thevenin 1961: 15), W. H. Purvis of Honokaa, Hawaii, introduced the species, as *M. ternifolia,* which he planted at Kapulena. A second introduction into Hawaii was made in 1892 by E. W. and R. A. Jordan who planted the trees at the former's home on Wyllie Street in Honolulu (Pope 1929:2). This introduction became the source of the principal commercial varieties cultivated in Hawaii today.

M. tetraphylla

VERNACULAR NAMES: Macadamia nut; rough-shell macadamia; spiny leaf macadamia; rough-shell Queensland nut; Australian nut; bush nut.

INDIGENOUS RANGE: Tropical rainforests on the eastern slopes of the Great Dividing Range, extending from the Richmond River near Casino and Lismore in northeastern New South Wales to the Coomera River in the vicinity of Beechmont and the Nerang River in the vicinity of Advancetown in the southeastern corner of Queensland, a distance of about 75 miles; latitudinal range, about 29°–28° S.

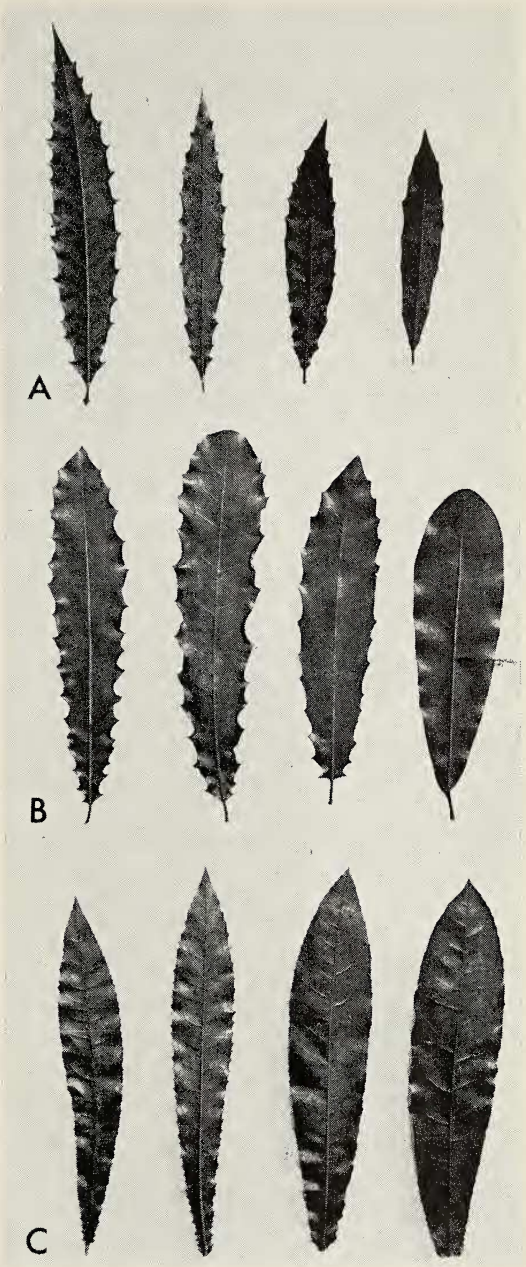

FIG. 3. Leaf transitions in *Macadamia* species, from juvenile on the *left* to adult on the *right. A, M. ternifolia; B, M. integrifolia; C, M. tetraphylla.*

The trees of this species are large and spread-

ing, sometimes attaining a height of 50 feet and a spread of 60 feet. The branchlets are usually dark colored, although not quite so dark as those of *M. ternifolia.* The young leaves on new growth are generally flushed with red or pink coloration. Occasional trees may be seen, however, which lack anthocyanin pigmentation and, consequently, have new leaves which are pale yellowish green in color. Juvenile leaves are long, linear-lanceolate. Adult leaves differ little from juvenile leaves except in being somewhat broader (Fig. 3*C*). Adult leaves measure 4–20 inches in length and 1–3 in width. They occur most commonly in whorls of four, although an occasional branch may have three or five; and, in young seedlings, they generally occur in opposite pairs. The racemes are borne in the proximal axils of the most recently matured two or three increments of growth. The racemes vary from 6–18 inches in length, and the number of flowers from 100 to 300 (Fig. 1). In the vast majority of trees the flowers are bright pink. In the occasional individuals which lack anthocyanin, however, they are white or cream colored. The crop matures from March to June in Australia, from March to June in Hawaii, and from September to January in California. There is no tendency toward everbearing in this species, consequently the entire crop is seasonal.

This species, as noted previously, was not recognized as new and different from *M. ternifolia* until 1954, when it was so recognized by Johnson (1954:15). By this time it had been in cultivation, as *M. ternifolia,* for 84 years. There is little doubt that it is the one referred to by an anonymous writer in 1870. Its introduction into commercial orcharding occurred about 1890, with the planting of about 250 trees on the K. C. Fredrickson property at Rous Mill, N.S.W. I visited this orchard, which is still in production, in 1960. The species was introduced into Hawaii by the Board of Agriculture and Forestry of the Government of Hawaii in 1892–94 for use in reforesting the slopes of Mt. Tantalus back of the city of Honolulu (Pope 1929:2). There seems to be no record of when and by whom it was introduced into California. The oldest trees I have seen appear to be 50–60 years old. They occur only in San Diego, Orange, and Los Angeles counties in southern California.

CYTOLOGY AND GENETICS

All three species have the identical somatic chromosome number of $2n = 28$. Insofar as I know, this report is the first on the chromosome numbers of *M. ternifolia* and *M. tetraphylla.* I determined these numbers from root tips of *M. ternifolia* and *M. tetraphylla* seedlings, and from dividing microsporocytes in *M. tetraphylla.*

The chromosome number of *M. integrifolia* was first reported (Darlington and Wylie, 1955:90) as "2n = 28 (56)," as a previously unpublished number determined by Ukio Urata of the University of Hawaii. The 56 in parentheses refers to a clone, Y-279, which was discovered to be tetraploid. Later, Urata (1954: 12) published the numbers as "n = 14 and n = 28," under an old, lapsed synonymous name, *M. ternifolia* F.v.M. var. *integrifolia* (Maiden and Betche) Maiden and Betche. I am familiar with Urata's material, since I served on the committee for his Master of Science thesis which served as the basis for the publication cited. The chromosome number reported for this species is confirmed in a recent paper by Ramsay (1963:9).

Johnson (1954:18), Beaumont (1956:17), and Smith (1956:40), have pointed out that a number of trees occurring in the Numinbah Valley and in tributary valleys of the Coomera River in southernmost Queensland have characters which strongly suggest that they are hybrids between *M. integrifolia* and *M. tetraphylla.* The region in question is the one in which the ranges of the two species come together and overlap to some degree. Beaumont collected cuttings of several specimens in 1953, which he sent to Hawaii and California to be propagated. These have flowered and fruited in recent years and, from close observations on them, there seems to be every reason to believe that they are indeed hybrids. Meanwhile, similar trees have been found in Hawaii and California among seedlings produced from seeds collected in orchards where the two species

grow together (Hamilton and Fukunaga, 1959: 7). Despite their putative interspecific hybrid origin, such trees are highly fertile.

Although the natural range of *M. ternifolia* lies completely within that of *M. integrifolia,* the two species are not found growing together. Nothing which might be construed to be a natural hybrid between them has been reported. I know of no attempt which has been made up to the present to hybridize *M. ternifolia* with either *M. integrifolia* or *M. tetraphylla.* Consequently its cross fertility with those species and the fertility of any hybrids which might be produced is unknown.

GRAFT COMPATIBILITY

Recent experiments in grafting have shown that the three species are mutually graft-compatible in any combination, whether used as rootstocks or scions (Storey and Frolich, 1964: 54–58). The degree of compatibility is so high that there is no observed tendency of any one species to overgrow the other at the graft union.

All attempts to graft *M. integrifolia* and *M. tetraphylla* on *M. prealta* and *M. whelani* have failed. Attempts to graft those species on *Grevillea robusta* A. Cunn. and *G. banksii* R. Br., closely related species in the family *Proteaceae,* also have failed.

SUMMARY AND CONCLUSIONS

This paper enumerates the ten species which comprise the genus *Macadamia* as it is presently understood. These fall into four clear-cut intrageneric groups. Species identification and typification in three of the groups have given no difficulty to systematic botanists and horticulturists in the past. The fourth group, however, which consists of the three species *M. ternifolia, M. integrifolia,* and *M. tetraphylla* and is commonly referred to as the "ternifolia group," was a source of confusion taxonomically for almost a hundred years.

Much of the confusion among the species undoubtedly resulted from the fact that everything that was collected in the field in the early years was placed under *M. ternifolia* in the herbarium. It is understandable how botanists working on such material in the herbarium came to regard *Macadamia* as a single highly polymorphic species, especially when one considers the overlapping ranges, the similarity of juvenile shoots and leaves, the transitional forms of leaves between the juvenile and the adult, and other factors, added to which is the possibility that the collections included some interspecific hybrid material. It is noteworthy, however, that most of the confusion and uncertainty one experiences from the study of pressed herbarium specimens is dispelled when he sees the trees in the field, for the species are so different in size and aspect that there is little doubt about their being distinct taxons.

That the three species are indeed closely related in a group set apart from the other species of *Macadamia* is attested by their high degree of mutual graft compatibility, by identical chromosome numbers, by the genetic cross-compatibility between two of the species, and by the high order of fertility of the interspecific hybrid. One can speculate that they arose from a single ancestral intrageneric prototype, and that the characters which distinguish one from another represent accumulations of gene changes over a long period of time which have not, however, affected chromosome homology. The occurrence of fertile hybrids is of interest, because it opens the way to genetic studies and to the possible improvement of horticultural varieties in a plant breeding program.

Superficially, the natural habitats of the species appear to be identical, and their natural requirements with respect to rainfall and soil factors to be the same. *M. integrifolia* and *M. tetraphylla* are often grown side by side in orchards in Australia, Hawaii, California, and elsewhere. In Australia cultivated trees of the former are to be seen as far south as Sydney. Trees of the latter are to be seen as far north in Queensland as Rockhampton. A matter for conjecture, therefore, is why the natural range of each is restricted to a comparatively small region, and why the ranges end so abruptly where they come together immediately north of the McPherson Range. This should make an interesting study in plant ecology.

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